Nemocataegis, a new genus and two new species of relictual seguenzioid gastropods (Vetigastropoda: Cataegidae) and a geobiological framework for integrating patterns in Deep Marine Wallacea

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ABSTRACT

Nemocataegis new genus, type species *N. mcleani*, is proposed for two elaborately sculptured, small-shelled cataegid gastropods from separate deep-water basins in the Indonesian biogeographic realm of Wallacea. The type species is from 885 m in the Gulf of Bone, between the southern and southeastearn arms of Sulawesi where the narrow gulf opens into the Flores Sea. The second species, *N. quinni*, is from 503 m in the Molucca Sea adjacent to Halmahera. Both species have the oblique, broadly expanding aperture, fluted outer lip and strong spiral cords characteristic of *Cataegis* McLean and Quinn, 1987, but shells are smaller (<20 mm) and the spiral cords are densely nodose, with fine axial ribs connecting the nodes and a unique microsculpture of fine threads and intritacalx in the channels between node rows. A previously described true *Cataegis* is endemic to the Makassar Strait in Wallacea, occurring at depths in excess of 1000 m. Cataegidae is re-diagnosed to include two genera, six nominal living species and two nominal fossil species. The family is assigned to Seguenzioidea based on a combination of morphological and molecular data. The new genus is endemic to Deep Marine Wallacea, and the new species occur in geographically isolated basins. Along with previously described deep-water gastropods in geologically ancient clades, they contribute to evidence of relictual biotas. The biogeographic patterns are correlated with factors that include the tracks of collecting expeditions, submarine topography, biogeographic lines, patterns of oceanic circulation, distribution of volcanic arcs and subduction zones, and major structural features resulting from tectonic collision, fragmentation, suturing, deformation, and extension over a period of more than 50 million years.

Additional Keywords: Sulawesi, Halmahera, Molucca Sea, Makassar Strait, Banda Arc, biogeography, hydrocarbon seep, deep sea, endemism, biogeography, systematics.

INTRODUCTION

This is the third in a series of papers describing unusual and relatively large-shelled (>20 mm) deep-water (200–2000 m) gastropods from three basal vetigastropod families.

Remarkably, the specimens are from expeditions and museum collections in which they may have been so unusual that they were incorrectly filed, misidentified, or simply waiting for resolution of the confused state of the taxonomy of fossil and living basal gastropods that have been variously arranged under many names at the "archaeogastropod" grade of evolution.

The first paper in the series (Hickman, 2012) described a new genus and two new species in the family Gazidae Hickman and McLean, 1990. It included anatomical and radular features as well as new shell characters. The second paper (Hickman, 2016) described eight species in the family Calliotropidae Hickman and McLean, 1990. Both papers are focused on the Indo-West Pacific Region and explore the complex geologic history of tectonic plate interactions, arc volcanism, subduction, accretion, and hydrography that identify a marine geobiogeographic realm designated here as "Deep Wallacea."

Deep Wallacea is distinct from the original terrestrial biogeographic concept that originated with Alfred Russel Wallace when he drew his famous line. Ironically, the region between Wallace's Line and Weber's Line was named "Wallacea" by geologist and paleontologist Roy Ernest Dickerson in an overlooked paper (1924: 3, fig. 1) designating "(1) the Asian (Sunda) Shelf, (2) Wallacea, and (3) the Australian Sahul Shelf (as) the three well-defined divisions of the Australasian Mediterranean Sea."

The primary objective of this paper is taxonomic: to describe a new genus and two new species of extant deep-water cataegid gastropods and to revise the diagnosis of the family. A secondary objective is to provide a set of maps and discussion of factors correlated with the disjunct and relictual distribution patterns of basal marine gastropods in Deep Wallacea. These include the tracks of collecting expeditions, the path of the Indonesian Throughflow and patterns of oceanic circulation, the division of the region into many separate basins and sub-basins, the distribution of active volcanoes and volcanic arcs associated with crustal collision

and subduction, and the distribution of major structural features and terranes that record a long geologic history of dramatic change in the distribution of land and sea.

A brief background of the ecology of living cataegids, their paleontological record, and their previous classification follows as an introduction to the systematic treatment.

Ecological Background

Living cataegid gastropods have been reported previously from bathyal depths (>200 m) in two widely separated regions of the world: (1) the combined basins of the Caribbean Sea (McLean and Quinn, 1987; Warén and Bouchet, 1993, 2001; Gracia et al., 2001) and Gulf of Mexico (McLean and Quinn, 1987; Warén and Bouchet, 1993, 2001; Carney, 1994; Cordes et al., 2010) in the Americas and (2) basins in the Southwestern Pacific that include the South China Sea (Fu and Sun, 2006), Wallacean Indonesia (McLean and Quinn, 1987), and Vanuatu (Kano, 2007; Warén, 2001). Complex active tectonism in these regions has produced some of the same geologic settings and features (subduction zones, thick accretionary prisms and melange, fault zones, mud volcanoes) that in turn give rise to unusual ecological settings. While geologists have focused on fluid expulsion in these settings (sulfides, petroleum, and other hydrocarbons, especially methane), biologists have focused on the ecological communities exploiting chemical energy via chemosynthesis.

Living cataegid gastropods consistently are associated with cold seeps where conduits for sulfide- and methane-rich fluids are expelled. In these environments microbial chemosynthesis creates both a rich nutritional source and a challenging oxygen-depleted setting for development of an extremophile macrobiota. In the Gulf of Mexico cataegids are linked to specific sulfide and hydrocarbon seeps off Louisiana (Carney, 2004; Cordes et al., 2010) and in the Caribbean in the thick accretionary prism off Venezuela, Trinidad, Barbados and Colombia (Gracia et al., 2001; Gill et al., 2005).

Fluid expulsion may also include barium-rich water that precipitates at oxic/anoxic boundaries as barium sulfate and barite sheets, mounds, cones and chimneys where a cataegid is part of a unique seep community (Cordes et al., 2010). The cataegid collected in the volcanic arc of Vanuatu was associated not only with cold seeps and hydrothermal vents, but also was reported as common on sunken wood (Warén, 2011).

Paleontological Background

Fossil specimens all occur in cold-seep carbonates and represent a broader geographic range that includes Lower Cretaceous (Valanginian) rocks in California (Kaim et al., 2014), and Upper Cretaceous (Campanian) rocks in Japan (Kaim et al., 2009; Kiel, 2010). Kiel and Campbell (2005) note that "trochomorph" gastropods that are abundant in some Lower Cretaceous cold-seep limestones in California are difficult to classify without original shell material.

At the boundary between the South American and Caribbean plates, collection records of *Cataegis meroglypta*

are more numerous from Paleogene and Neogene seep carbonates than from modern seeps in the region (Gill et al., 2005), although this is potentially biased by greater sampling effort in the fossil record. The record of Cenozoic seep faunas in the Caribbean has been extended to sites in the Dominican Republic and Cuba (Kiel and Hansen, 2015).

The number of species is likely to increase with recognition of fossil shells described under other names in early literature. Kaim et al. (2014) note the morphological similarity of a species described as *Phasianema taurocrassum* Sacco, 1895 from the Miocene "*Calcare a Lucina*," classic seep limestone chemoherms (Moroni, 1966; Taviani, 1994) in the Appenine chain of the Italian peninsula. Of special note is a species from Trinidad described as *Solariella godineauensis* by Katherine VanWinkle (1919), who noted (p. 26) both a flaring aperture and crenulated carinae. Kiel and Hansen (2015, fig. 14E) provide an excellent image that clearly shows seguenzioid axial threads in the interspaces between spiral cords.

Nomenclature and Classification of Cataegid Gastropods

The genus *Cataegis*, along with the family Cataegidae, is a relatively late addition to the large global inventory of vetigastropods. The family group was originally described and treated as a trochid subfamily of uncertain affinity (McLean and Quinn, 1987; Hickman and McLean, 1990; Warén and Bouchet, 1993). In a transformative, new working gastropod classification (Bouchet and Rocroi, 2005), the family was tentatively reassigned to Seguenzioidea along with Calliotropidae and Chilodontidae. This new view of Catageidae is supported by molecular data (Kano, 2007; Kano et al., 2009; Aktipis and Giribet, 2012), although the cataegid sequence used in all three analyses (*Cataegis* sp.) is, unfortunately, not tied to a shell voucher specimen. Prior to this report there were four nominal species of cataegid gastropods, all described under *Cataegis*: two from the Caribbean (McLean and Quinn, 1987), one from Indonesia (McLean and Quinn, 1987) and one from the South China Sea (Fu and Sun, 2006).

Paleontologists have recognized fossil *Cataegis* specimens as seguenzioid without further classification (e.g. Kiel and Hansen, 2015), or with assignment to Catageinae as a subfamily of Chilodontidae Wenz, 1938 (Kaim et al., 2009; 2014).

SYSTEMATICS

Subclass Vetigastropoda Salvini-Plawen, 1980
Seguenzioidea Verrill, 1884 (unranked)
Eucycloidea Koken, 1897 (unranked)
Family Cataegidae McLean and Quinn, 1987

Genus *Cataegis* McLean and Quinn, 1987

Type Species: *Homalopoma finkli* Petuch, 1987 (senior synonym of *Cataegis toreuta* McLean and Quinn, 1987).

Recent, Gulf of Mexico, Caribbean and Western Atlantic; at continental slope depths, 337–1283 m.

Remarks: McLean and Quinn (1987) based the family group and genus primarily on a highly unusual radula in the type species. The rachidian was missing, the innermost laterals lacked cusps and were elaborately fused, and remaining three laterals had small cusps but complexly interlocking shafts and bases. Hickman and McLean (1990) suggested that the radula represented "an evolutionary excursion in the direction of disorder." It was therefore surprising when Warén and Bouchet (1993: fig 14C) figured a radula from *C. meroglypta* McLean and Quinn, 1987 with a robust rachidian tooth with a well-developed and sharply-edged cusp. Habitat data help make sense of the radular disparity, because *C. meroglypta* occurs on hard substrates at methane seeps and feeds on bacterial films, whereas the type species is reported to feed on sunken and decaying seagrass (Warén and Bouchet, 1993). Although radular morphology is usually the best indicator of suprageneric placement, the cataegid shell is unusually rich in characters that are used here to supplement the original description of the family group and to accommodate a second genus, *Nemocataegis*, for which the radula and anatomy are unknown.

Three unique characters, in combination, were specified as diagnostic of the family group and genus (McLean and Quinn, 1987: 111–112): strong spiral cords, lack of columellar plications, and the oblique, broadly expanding aperture. Additional characteristic features include the deep, concave spiral interspaces lined with extremely fine prosocline or slightly sinuate axial threads and a dense microsculpture of discontinuous, reticulate or anastomosing, ridges and grooves that are infilled or overprinted by a chalky or crumbly brownish intritacalx (sensu D'Attilio and Radwin, 1971). The intritacalx may be so extensively developed as to obscure the microsculpture, but it clearly is not a continuous periostracal sheet. Intritacalx is also an important microstructural feature in two other seguenzioid families: Eucyclidae (Herbert, 2012) and Calliotropidae (see Hickman, 2016, for a discussion).

Macroscopic axial sculpture in *Cataegis* is restricted to elongate, fine nodules on the spiral cords. In all cataegids the columella is thickened, arcuate, lacking plications or teeth and covered with a thin callus that extends to cover the umbilicus completely or to leave a narrow umbilical chink. Interior nacre is not covered with a translucent inclined prismatic layer as in some seguenzioids, and it does not extend all the way to the growing margin of the shell, even in adults with descending sutures and final apertures. Spiral ornament is visible through the interior nacre as ridges and grooves. Fluting of the outer lip at the termination of spiral ridges and grooves is also characteristic of the family.

Genus *Nemocataegis* new genus

Type Species: *Nemocataegis mcleani* new species.

Description: Shell small for family (height <15 mm), turbiniform, low spired, with rapidly expanding body whorl and large, oblique aperture; spiral ribs increasing by intercalation to >10 on body whorl and crossed by numerous thin, continuous, prosocline axial threads that form elongate nodes or sharp scales on spiral ribs; spiral groves with microscopic sculpture and brownish intritacalx; columellar lip arcuate, smooth, and thickened by opaque callus; callus almost completely covering umbilicus as well as extending into interior margins of basal and apertural lips and covering nacre; adult suture and aperture descending; interior nacre with weak ridges and grooves reflecting exterior spiral sculpture.

Remarks: The new genus is clearly distinguished from *Cataegis* by its smaller shell size (<15 mm), more numerous, narrower, and prominently-beaded spiral cords, narrower spiral interspaces, lack of continuous periostracum, and well-developed intritacalx in microscopic grooves between crowded axial microsculptural threads.

It is unfortunate that the protoconchs are worn and that there are no data on the anatomy or radula. It is remarkable that the empty shells are so exquisitely preserved, and it is possible that the well-developed intritacalx has served a protective function against dissolution. Shells show no sign of encrustation, but there is evidence of repaired breakages. The known specimens come from gray mud at slope depths and are most likely deposit feeders.

Etymology: *Nemo* (Gr. thread) + *Cataegis*, in reference to the fine axial sculpture that distinguishes the threaded cataegids.
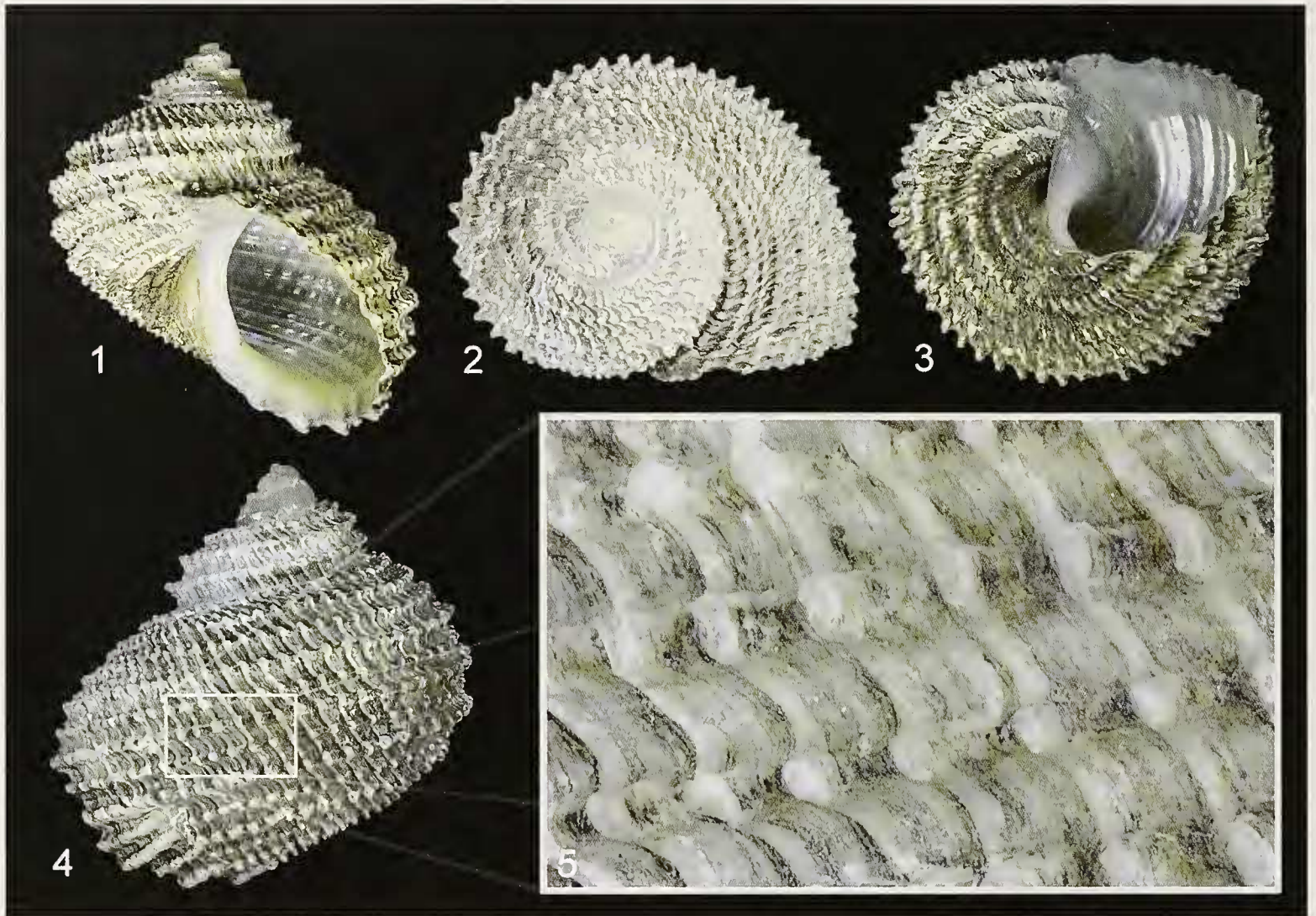
Nemocataegis mcleani new species
(Figures 1–5)

Diagnosis: Enlarged body whorl evenly rounded, without peripheral or basal demarcation; 6 primary spiral cords visible in apical view, 5 additional spiral cords visible in umbilical view; secondary spiral cords intercalated between primary adapical spiral cords; axial ribs forming short, sharp, anteriorly directed spines on primary and secondary spiral ribs; thin callus deposit covering interior nacre on outer and basal lips overlapping columellar callus at base and top.

Description: The type species of *Nemocataegis* is clearly distinguished from *N. quinni* new species (described below) by more numerous primary spiral cords and more prominent, sharp, spinose projections where they are crossed by axial threads. The short spines are incompletely closed and project anteriorly (Figures 2, 3). In the deep spiral grooves the depressions between axial threads are filled with intritacalx that either obscures underlying structure or shows faint axial lineation (Figure 5).

Holotype: USNM 239464, height 14.4 mm, maximum width 14.0 mm.

Figures 1–5. *Nemocataegis mcleani* new species. **1.** Semiapertural, **2.** Apical, **3.** Basal, and **4.** Abapertural views of holotype, USNM 239464, height = 14.4 mm. **5.** Detail from Figure 4 of nodose axial ribs and closely-spaced threads filled with brownish intritacalx.

Type Locality: 03°17′40″ S, 120°36′45″ E, Gulf of Boni (Bone), Celebese (Sulawesi), SE of Olang Point, 484 fathoms (=885 m), U.S. Fish Commission, R/V ALBATROSS, Station 5656, 19 December 1909, gray mud.

Distribution: Known only from the type locality.

Etymology: Named for the late James H. McLean in recognition of his many important contributions to understanding basal marine gastropods.

Remarks: The holotype appears to be an adult specimen on the basis of terminal growth features that include a descending suture and terminal translucent callus covering, but not totally obscuring, nacre inside the outer lip (Figure 3). Height and width are effectively equal. A major breakage in the basal portion of the outer lip (Figure 4) is repaired by a partially disjunct continuation of sculpture. The shell is remarkably fresh in appearance and was not encrusted by epizoans in the manner common to many calliotropids, especially those living on hard substrates.

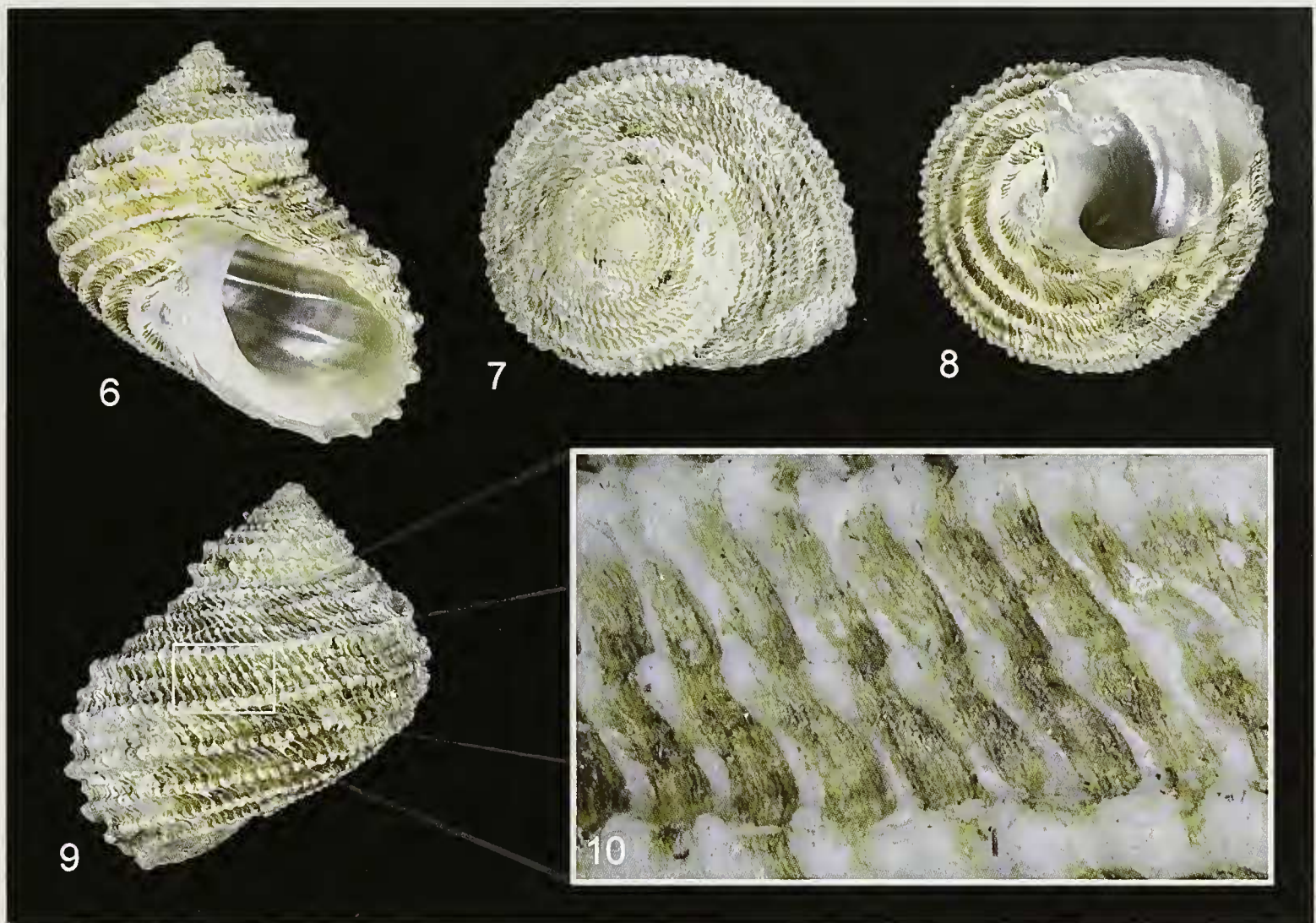### *Nemocataegis quinni* new species
(Figures 6–10)

Description: Enlarged body whorl with slightly concave shoulder slope; final aperture strongly oblique, with descending suture; spiral ribs of unequal strength and spacing, interspaces broader than ribs; numerous fine axial threads producing small blunt nodes at intersection with spiral ribs; brownish intritacalx well developed between axial threads in spiral interspaces; columellar callus reflected and covering umbilical region; columellar lip strongly arcuate, callus extending into aperture, partially obscuring interior nacre; interior nacre with weak spiral ridges.

Holotype: USNM 239279. Height 14.0 mm, maximum width 13.4 mm.

Type Locality: 00°19′20″ N, 127°28′30″ E, Molucca Sea, Halmahera, off Makian Island, 275 fathoms (=503 m). U.S. Fish Commission, R/V ALBATROSS, Station 5622, 29 November 1909, gray mud.

Distribution: Known only from the type locality.

Figures 6–10. *Nemocataegis quinni* new species. **6.** Semiapertural, **7.** Apical, **8.** Basal, and **9.** Abapertural views of holotype, USNM 239279, height = 14.0 mm. **10.** Detail from Figure 4 of nodose axial ribs and closely-spaced threads filled with brownish intritacalx.

Etymology: Named for James F. Quinn, Jr. in recognition of his insightful contributions to the systematics of deep-sea gastropods.

Remarks: This species is distinguished from the type species by its more numerous, shorter and bluntly rounded nodes on the spiral ribs, a completely obscured umbilicus, slightly convex shoulder slope on the body whorl, more strongly descending final aperture, and less visible traces of spiral sculpture in the interior nacre. The terminal growth features on the shell of the holotype suggest that it is an adult. The brownish intritacalx (Figure 10) is well developed in axial interspaces over the entire shell except at the apex. The protoconch small, but sufficiently worn that the boundary with the worn early teleoconch whorls cannot be discerned.

DISCUSSION

In light of pronounced under-sampling of the deep-water fauna of Wallacean Indonesia, it is remarkable that the region contains so many species and higher taxa that have never been recorded in relatively well-sampled regions of the Indo-Pacific. The endemic genus and two new species of Cataegidae described above join a diverse assemblage of basal gastropods that includes an endemic genus of Gazidae (Hickman, 2012) and six recently-described large-shelled species of Calliotropidae (Hickman, 2016).

Adequate sampling of the deep Wallacean fauna requires a protocol that recognizes factors that appear to be contributing the accumulation of relictual taxa. The primary purpose of this discussion is to extend previous characterization of deep Wallacea (Hickman, 2009a; 2009b; 2009c; 2012; 2016) and to provide a set of graphic illustrations (Figures 11–16) of the interacting components of deep Wallacean complexity.

This narrative begins with the currently known occurrences of species with deep (Paleozoic or Mesozoic) evolutionary origins and endemic or strongly disjunct representation in separate basins within Wallacea. It proceeds with components of explanation that are consistent with the objectives and tracks of previous collecting expeditions, the basins and sub-basins of Deep Wallacea, shallow oceanic circulation and path of the Indonesia Throughflow, the distribution of active volcanoes and

volcanic arcs, and the distribution of trenches, faults, and major tectonic features that are essential to understanding the geologic history of changing distribution of land and sea.

The term "Indonesian Archipelago" (the Malay Archipelago of Wallace, 1860; 1863; 1869) is a misnomer. A modern map Indonesia at the scale typically used to depict the islands of Oceania misses most of the more than 17000 islands and their arrangement. The region is actually a composite of separate archipelagic seas, straits and gulfs that have opened, expanded, contracted, and in some instances disappeared over a 200 My geologic history that began with the break-up of Gondwana (Metcalfe, 2011). The larger islands in these seas have likewise moved, collided, fused, separated or disappeared during the tectonic evolution of the region. Many islands have emerged or submerged during its more recent eustatic history. The biogeographic effects of sea level change during the Pliocene and Pleistocene have received considerable attention from terrestrial and shallow marine biogeographers. Regional biogeography still lacks a deep marine perspective. Appreciation of the paleobathymetric complexity of the Wallacean seaways is, however, of increasing interest to physical oceanographers and meteorologists investigating large-scale influences of ocean circulation on global climate (e.g., Cane and Molnar, 2011).

Endemic and Relictual Taxa in Wallacea

Occurrences of cataegid gastropods in deep Wallacea are illustrated in red in Figure 11, along with occurrences of calliotropid (green) and gazid (blue) vetigastropods, abyssochrysid gastropods (yellow), and a living coelacanth fish (star). Previous discussion (Hickman, 2016) of the deep geologic origins (Paleozoic or Mesozoic) and pronounced global disjunctions in these groups are consistent with the hypothesis that they are relictual taxa. The fossil records of more widespread geographic occurrence and greater taxonomic diversity are similarly indicative of a concentration of relictual taxa in Deep Wallacea.

Expeditions and Benthic Sampling Coverage

Within Wallacea, the distributions shown in Figure 11 are correlated with the tracks of the Dutch SIBOGA Expedition of 1889–1900 and the R/V ALBATROSS Philippines Expedition of 1907–1910 (Figure 12). Although both expeditions produced remarkable oceanographic data, dredge samples, and new marine taxa from >200 meters, the research objectives were different in intent and execution as well as in their subsequent study and publication of results.

The SIBOGA Expedition was conducted under the leadership of Professor Max Weber, a distinguished zoologist at the University of Amsterdam, whose proposed track (shown in orange in Figure 12) was a zig-zag exploration of the margins of the region of deep marine basins between the Sunda and Sahul continental shelves.

His proposed track was not followed precisely, but it appears to reflect Weber's curiosity about the terrestrial biogeographic lines that recently had been drawn by Wallace (1863) and Lyddeker (1896) and their potential oceanographic correlates. The commander of the SIBOGA, G.F. Tydeman, was expert at recording deep soundings and oceanographic data (Tydeman, 1903) from the >300 sampling stations. Most remarkably, the taxonomic results were published in a series of >100 monographs and included descriptions of the prosobranch gastropods (Schepman 1908; 1909). For a summary of the SIBOGA and other Dutch Oceanographic research in Indonesia in colonial times, see Van Aken (2005). The specimens were from both shallow and deep stations on the periphery of the region, and the SIBOGA did not sample in the gulfs, basins, and sub-basins of Sulawesi and Halmahera.

The ALBATROSS Philippines Expedition was designed as a focused survey of the aquatic resources of the Philippine Islands, under the command of Hugh McCormick Smith of the U.S. Bureau of Fisheries. It was conducted as a series of cruises, with the addition of a final two months in the Dutch East Indies (Indonesia) at the end. The major biological reports are on the fishes (see Smith and Williams, 1999). The track of the ALBATROSS in Indonesia is shown in purple in Figure 12).

Little is known about the objectives or why the cruise was narrowly focused on obtaining collections and data from deep stations in Sulawesi (Makassar Strait, Gulf of Bone, and Gulf of Tomini) and the western margin of Halmahera. Malacologist Paul Bartsch, who had represented the Smithsonian Institution in the preceding Philippines cruises, left the expedition before it departed for Indonesia. Hugh McCormick Smith also had departed, and there is no record of who was in charge. What little we do know is from the autobiography of Roy Chapman Andrews, who was recruited as a 24-year-old graduate student and charged with terrestrial collecting. He notes (Andrews, 1943: 67) that "It wasn't a 'happy ship'" and that he was "supposed to have no part in the dredging operations" (p. 72). He makes no mention of marine mollusks in his romanticized account.

In spite of what little is known samples were obtained from 72 stations between 7 November and 30 December 1909. Specimens and station data were meticulously processed and accessioned into the Smithsonian mollusk collection and archives and are still being discovered and studied by malacologists with expertise in various taxonomic groups.

With the exception of the SIBOGA Expedition and its monumental series of reports, oceanographic research during colonial rule in Indonesia has been characterized as a "gunboat science" (Van Aken, 2005). However, Van Aken's (2005) summary highlights many important hydrographic, physical and chemical oceanographic, and geophysical data that were obtained and published by dedicated scientists who obtained private funding.

A limited biological sampling effort in 1922 in the vicinity of Kai and Tanimbar was aimed at evaluating a proposed Danish tropical marine station (Mortensen,
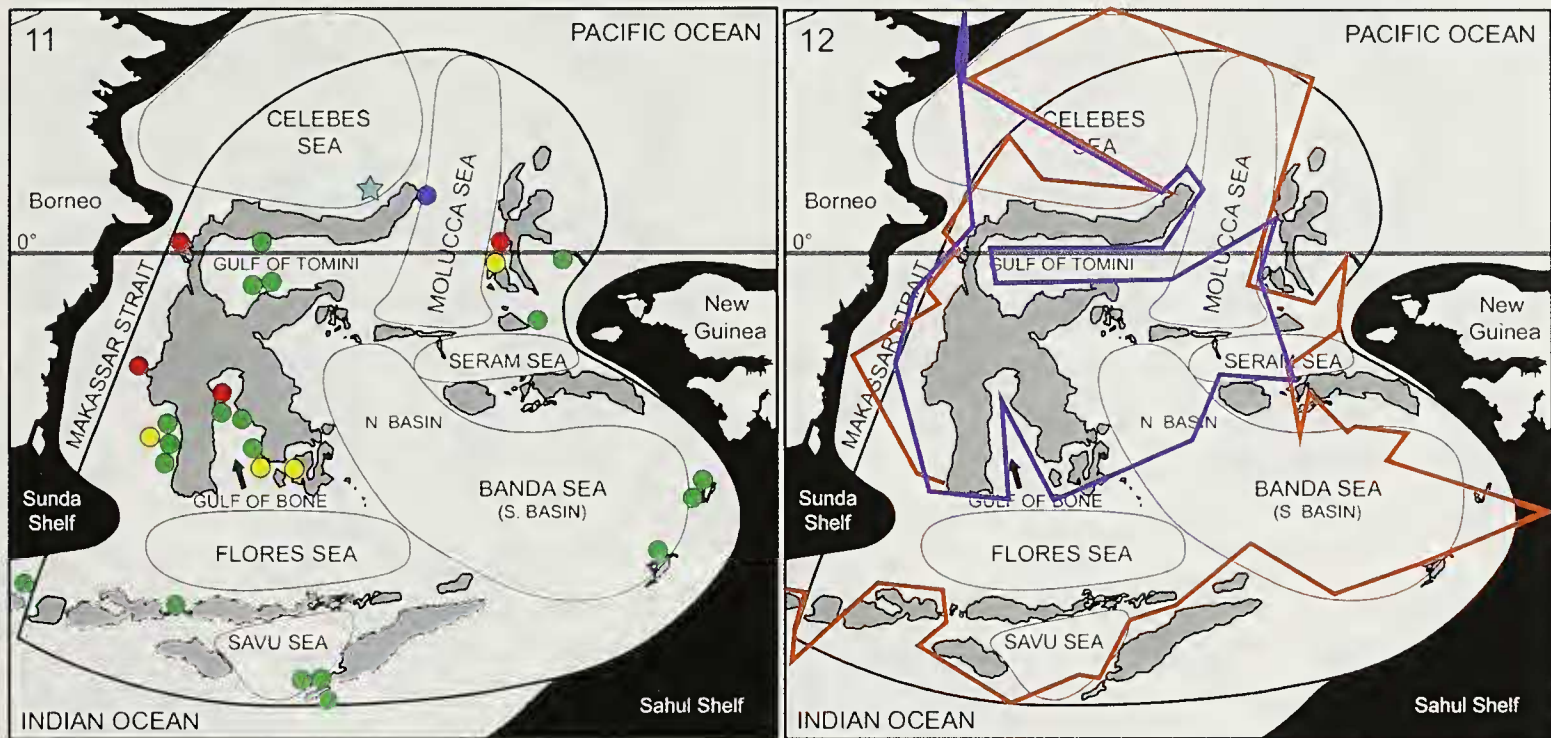
Figures 11–12. Simplified maps of marine Wallacea comparing occurrences of relictual deep-water taxa and tracks of major collecting expeditions. **11.** Collecting sites for cataegid (red circles), calliotropid (green circles), gazid (blue circle) and abyssochrisid (yellow circles) gastropods; and living fossil coelacanth fish (blue star). **12.** Tracks of the *Siboga* Expedition (orange) on the margins of Wallacea and the *Albatross* Expedition (purple) within northwestern Wallacea.

1923) and contributed no deep-water gastropods perti-nent to this discussion. The KARUBAR joint Indonesian and French cruise in this region, also sampled primarily at shallower depths (< 500 m) with a strong focus on the Arafura Sea (outside of Wallacea) rather than in the Banda Sea (Crosnier et al., 1997). An additional joint Indonesian and French sampling effort (CORINDON 2) (Moosa, 1984) sampled deep-water stations on either side of the Makassar Strait, adding a abyssochrysid records, including a new species (Bouchet, 1991).

BIOGEOGRAPHIC LINES AND THE EVOLVING CONCEPT OF WALLACEA

More than enough has been written about the drawing of lines by terrestrial biogeographers in the Indonesian re-gion (e.g., Mayr, 1944; Michaux, 2010). From a marine perspective, the margin of the Sunda Shelf to the west and margin of the Sahul shelf to the east define Wallacea as a region in precisely the manner originally intended by Dickerson (1924) when he proposed the term. Wallacea is illustrated here (Figure 13) as lying between the "Wallace Line and Weber Line slightly modified" (see Dickerson, 1924: fig. 1).

The Oceanographic Data Set for the ALBATROSS sampling in Indonesia includes 71 stations concentrated close to shore in four separate basins adjacent to Sulawesi and Halmahera (Makassar Strait, Gulf of Bone, Gulf of Tomini, and Molucca sea). These basins are shown in blue (Figure 13). In each setting, the 200 m isobath is very close to shore, and 56 of the stations sampled were from depths >200 m, 30 stations were from >1,000 m and 13 stations were from >1,500 m.

Restriction of marine fauna to individual basins, gulfs, and straits within Wallacea is consonant with the complex geological history of fragmentation and amalgamation in marine Wallacea as a whole. Similar recognition of multiple sub-regions of endemism in the terrestrial biota (e.g., Michaux, 2010) advances biogeographic analysis as an integration of distributional data with geotectonic history.

THE INDONESIAN THROUGHFLOW AND SHALLOW OCEANIC CIRCULATION

Patterns of distribution of marine invertebrates in Wallacea are typically examined in terms of the oceanic currents that transport and disperse pelagic larvae. Considerable emphasis has been placed on the potential importance of the In-donesian Throughflow (ITF) in determining patterns of genetic connectivity. The gateway connection between the North Pacific and the Indian Ocean (Figure 14) is a com-plex system of shallow and deep currents. The main route is a shallow southward flow of the Mindanao Current through the Celebese Sea and Makassar Strait. It enters the Indian Ocean between Bali and Lombok with another branch turning eastward through the Flores Sea, branching again to flow through the Banda Sea, entering the Indian Ocean through the Ombai Strait and Timor Passage on either side of Timor.

Minor secondary flow through the Molucca Sea and into the Banda Sea is more complicated. North Pacific water is initially deflected from reaching the Banda Sea by eastward reversal of flow in the South Equatorial Current (SEC) into the North Equatorial Counter Current
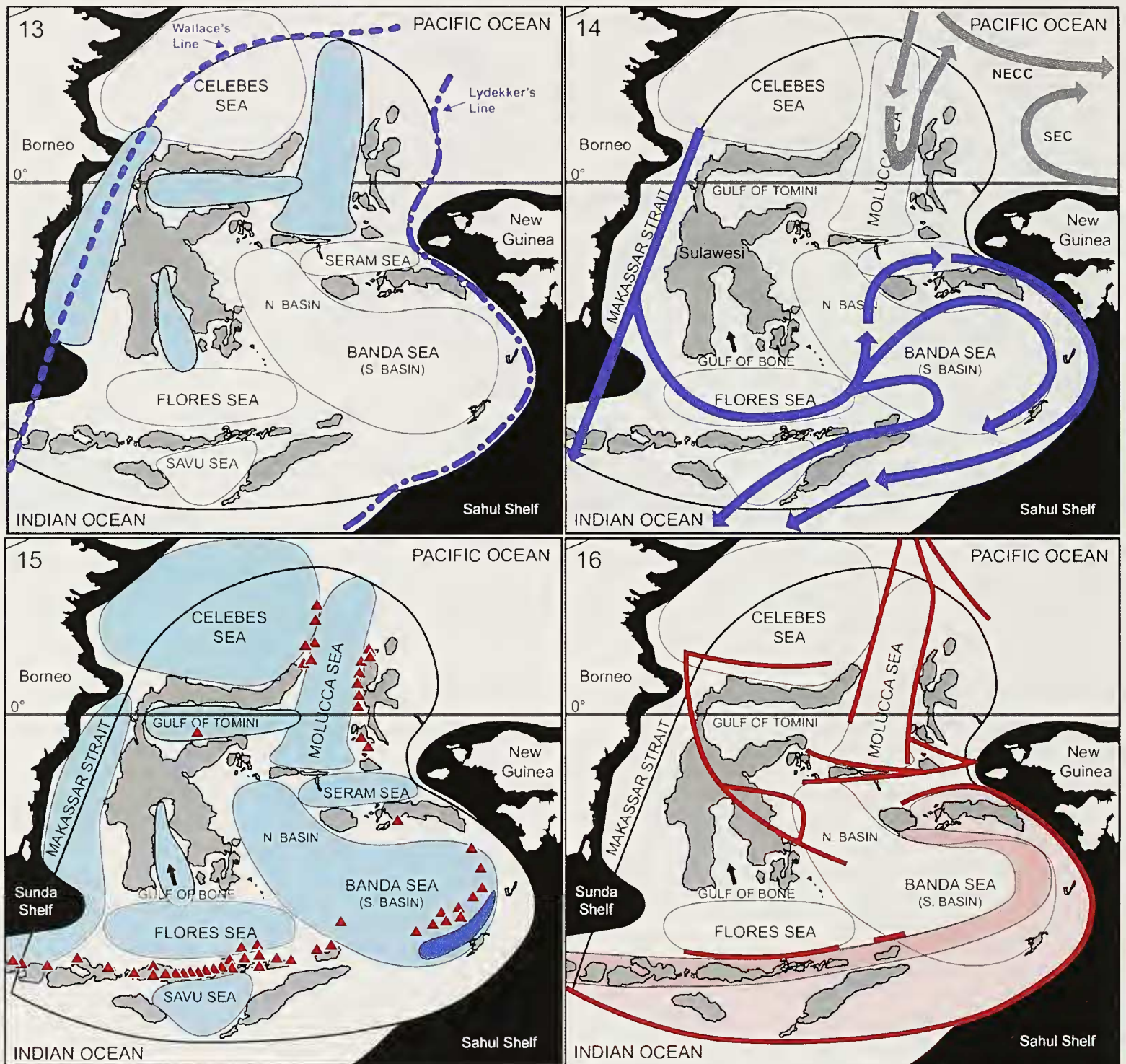
Figures 13–16. Simplified maps of factors correlated with occurrences of relictual deep-water taxa. **13.** Outline of Wallacea bounded on the west by Wallace's Line (purple dashes) and the east by Lydekker's Line (broken purple dashes), and the four deep basins (blue) from which the *Albatross* gastropod specimens were dredged: Molucca Sea, Gulf of Bone, Makassar Strait, and Gulf of Tomini. **14.** Surface currents of the Indonesian Throughflow (ITF) from the North Pacific through the Southeast Asian Gateway to the Indian Ocean and surface currents with no significant flow through Wallacea (gray). **15.** Nine major Wallacean basins underlain by oceanic lithosphere (blue), the anomalously deep Weber Basin (deep blue), and historically active volcanoes (red triangles) defining basin boundaries. **16.** Fault systems and subduction zones (red) associated with major tectonic terranes, and position of the outer (light pink) and inner (dark pink) zones of the Banda Arc.

(NECC) influenced by several large semi-permanent eddies (Arruda and Nof, 2003). Deeper flow entering the Banda Sea is further impeded by sills and physical barriers separating sub-basins (Gordon et al., 2003; Van Aken et al., 2009). The Banda Sea appears to contribute a relatively minor amount to total throughflow (Gordon and Fine, 1996). This is an oversimplification of

a temporally and spatially variable pattern that is incompletely characterized in spite of a growing body of detailed oceanographic data. The patterns of flow vary on time scales ranging from days and seasons to decades and significant periods of geologic time (Tillinger, 2011).

While the ITF (shown in Purple in Figure 14) and interactions with the boundary between major gyres and

eddies (shown in gray in Figure 14) may be significant factors in the dispersal and connectivity in the hyper-diverse shallow marine biota of Wallacea, they are less likely to play a role in understanding the endemism in deep-water cataegid, calliotropid, or gazid gastropods (Hickman, 2012, 2016). From an oceanographic per-spective, this is because deep-water current systems are different and from a biological perspective because deep-water vetigastropods lack a significant pelagic dispersal stage in their life history. They likewise have been un-affected by Pliocene and Pleistocene sea-level change and because they occur in basins that are isolated from one another by submarine topographic barriers that restrict the dispersal of benthic adults.

MARINE BASINS AND VOLCANIC ARCS

There are at least 26 bathymetrically distinct basins within the Wallacean region that reach bathyal depths (>200 m). The nine illustrated in blue (Figure 15) contain species of basal marine gastropods in clades associated with chemical energy sources. The Wallacean basins are al-ternatively identified in the literature and on maps as seas (*laut*), straits (*selat*), or gulfs (*teluk*). Straits are narrow passages between islands, while gulfs are deep inlets or indentations in the larger emergent landmasses, notably the Gulf of Tomini and the Gulf of Bone in Sulawesi. Complex ridge systems create bathymetric isolates in some of the basins. Examples in the Banda Sea include a main North Basin (Sula) and a South Basin that is further subdivided into the Wetar, Damar, and Weber basins. The Weber Deep (in dark blue) is an anomalous, tec-tonically generated bathymetric isolate in the Banda Forearc with depths exceeding 7 km. The Makassar Strait, the Bone Basin, and the Gulf of Tomini also contain bathymetrically distinct sub-basins. Although bathymetry and submarine topography can confine or restrict benthic taxa that lack a planktonic dispersal phase, bathymetric complexity must be further integrated with the geologic history. This is especially true of volcanic arc activity that has shaped basin development and the sedimentary component of deep-water ecosystems.

The link between geologic and ecologic settings in deep Wallacea has not been explored. Understanding the role of volcanic arcs in basin development, sedimentation, underlying stratigraphy, structure, geophysics, and geo-chemical peculiarities is crucial to understanding the deep benthic realm in which endemic and relictual taxa have accumulated. The major abiotic features of magmatic arc history (Hall and Smyth, 2008) provide a framework and starting point for future integrative study.

The modern volcanic arcs in Wallacea (Figure 15) are depicted by red circles representing volcanoes that have been active historically (Smithsonian, 2016). There are many more named volcanic edifices that are presumably inactive, and little is known of submarine volcanism.

The subduction zone system in Wallacea includes four volcanic arcs (Figure 15). The Sunda and Banda volcanic chains mark the zone of melting as the Indo-Australian plate is subducted beneath the Eurasian Plate. To the north, the Sanghe (or North Sulawesi Arc) and the Halmahera Arc mark the convergent margins of the formerly larger Molucca Sea Plate that is disappearing in a unique modern example of double subduction system. The con-striction of the formerly broad Molucca Seaway necessarily represents a constriction of deep marine habitat and is consistent with the occurrence of relictual molluscan taxa (Hickman, 2012; 2016).

Much of the basin formation in Wallacea appears to be driven by extensional rather than compressional tectonic forces (Charlton, 1991; Charlton et al., 1991; Hall, 2013; Pownall et al., 2013). These include the opening of both of the two deep interarm basins of Sulawesi: the Gorontolo basin in the Gulf of Tomini (Pholbud et al. 2012) and the Bone Basin in Sulawesi (Sudarmono, 2000). The im-portance of slab rollback and lithospheric extension in the Banda Arc is perhaps most dramatic in the proposed detachment model for formation of the Weber Deep (Pownall et al. 2016).

Further understanding of basin history requires ex-amination of subsurface structure, which is difficult to depict and interpret in simplified map view. The following section highlights some of the Wallacean structural fea-tures that are especially germane to the peculiar geo-graphic distribution of deep-water marine gastropods.

MAJOR STRUCTURAL FEATURES AND HISTORY

The major structural features of Wallacea (Figure 16) provide a starting point for understanding the complex history that is treated in a diffuse and evolving body of literature and lively debate over alternative interpretations (See Hall, 2011; 2013; Hall and Blundell, 1996); Hall and Wilson, 2000; Hall et al. 2011 and references therein). Full understanding of modern Wallacea requires going back to the Paleozoic break-up of greater Gondwanaland and tracing separation and movement of micro-continental fragments, the openings new ocean basins, the collision and suturing of slivers, translations and subductions, and disappearance of some of the features ultimately responsible for the modern distribution of tectonically bounded marine basins and terrestrial blocks and fragments (e.g., Metcalfe, 2001; 2011). Features depicted in red in Figure 16 include active trenches, major sutures, thrust faults, and strike-slip faults and fault zones.

The most prominent structural feature is the horseshoe-shaped Banda Arc (Figure 16), a complex suture zone in which multiple Jurassic to Neogene pre-collisional imbri-cate wedges are continuous with post-collisional evolution of the modern forearc (Charlton et al., 1991). The zones of folding and thrusting of the outer arc complex (successively older from southeast to northwest) and the modern deep forearc basin are represented in pink, in Figure 16). The Islands and volcanoes of the active inner arc are repre-sented in salmon. The Banda Arc is an exemplar of an arc-continent collision with multiple episodes of accretion of crustal blocks and fragments and is treated in an extensive

literature (e.g. Bowin et al., 1980; Charlton et al, 1991; Hall and Wilson, 2000; Harris, 2006; and references therein).

Three additional suture zones (Figure 16) are: (1) the Sulawesi Suture, also a complex region of multiple collisions, (2) the Sorong Suture, a major east-west trending fault zone of multiple collisions, and (3) the Molucca Suture where two colliding volcanic arcs are converging to close the ancient Molucca Seaway (see Hall and Wilson, 2000 for a review and references).

The relevance of the Wallacean suture zones to marine biogeography, endemism, and the deep-water relictual gastropod taxa resides in the clear evidence of geo-chemically unusual and extreme environments of interest to petroleum geologists, who have identified commercial hydrocarbon occurrences (Charlton, 2004), hydrocarbon seeps (Camplin and Hall, 2014) and mapped fields of mud volcanoes (Barber et al., 1986).

Biological expedition reports provide few clues to geochemical and sedimentary settings at sampling stations. However, the increasing geological evidence in deep Wallacea for both explosive and diffuse expulsion of fluids rich in sulfides and hydrocarbons (Hickman, 2016) are consonant with the presence of (1) taxa that have been identified elsewhere in the world as part of chemo-synthetically based communities, (2) adaptations to toxic fluids and hypoxia, and (3) nutrition based on elevated productivity of chemosynthetic microbes and microbial mats.

CONCLUSIONS

Understanding of the marine biogeography of Deep Wallacea is in its infancy. Distribution of relictual basal gastropod taxa is linked to features mapped in this paper: expedition tracks and biological sampling, positions of discrete marine basins and their topographic boundaries, patterns of ocean currents and circulation, distribution of active volcanoes and volcanic arcs, and distribution of what remains of the complex structural record of tecto-nism over many millions of years. A full geobiological history will emerge only through integrating data from the disparate sources and disciplines implicated above. At the same time, interdisciplinary exchange is likely to assist both geologists and biologists in addressing separate, discipline-specific questions. It is ironic that a paleontol-ogist should find herself attempting to unravel a deep-water geobiological history that has no preserved fossil record in Wallacea. However, it is those with formal training in both geology and biology who are most likely to be challenged and attracted to this kind of integrative effort.

ACKNOWLEDGMENTS

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